

Giant Ringtail Possums (*Marsupialia*, *Pseudocheiridae*) and Giant Koalas (*Phascolarctidae*) from the Late Cainozoic of Australia

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While seven pseudocheirids have been described from the late Oligocene to early Miocene and five from the Pliocene of Australia, none are known to have been confined to the Pleistocene. We describe here a giant ringtail, *Pseudokoala cathysantamaria* n. sp., from the early Pleistocene Portland Local Fauna (lower Nelson Bay Fm) of Victoria. We review the generic distinction of the Miocene-Pliocene *Corracheirus* Pledge, 1992 and conclude that it is a junior synonym of *Pseudokoala* Turnbull and Lundelius, 1970. The palaeohabitat for all species of *Pseudokoala* appears to have been rainforest. A second pseudocheirid in the Portland Local Fauna is most similar in morphology and size to the still-living *Pseudocheirus peregrinus*, a species whose habitat range also includes rainforest. We describe the first known upper and additional lower molars for the giant koala *Cundokoala yorkensis* Pledge, 1992, from a Pleistocene deposit in Wellington Caves, New South Wales, a taxon previously only known from Pliocene sediments of South Australia. The Portland giant ringtail and Wellington giant koala add two more families to the already extensive list that exhibited Pleistocene gigantism. Previously, only one other lineage (tree kangaroos) of arboreal mammals has been known to have undergone gigantism.

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KEYWORDS: Koalas, Phascolarctidae, Pleistocene gigantism, Pseudocheiridae, Quaternary, ringtail possums.

INTRODUCTION

The record for ringtail possums (*Pseudocheiridae*) begins in the late Oligocene. From sediments of this age in South Australia, Woodburne et al. (1987a) and Pledge (1987b) describe four species of *Pildra*, two of *Marlu* and one of *Paljara*. Archer (1992) reports over twelve additional unnamed taxa from the Oligo-Miocene sediments of Riversleigh, northwestern Queensland. Archer and Bartholomai (1978) note a *Pseudochirops* from the late Miocene of Alcoota, Northern Territory. Turnbull and Lundelius (1970; augmented by Turnbull et al. 1987) describe *Pseudokoala* from the early Pliocene Hamilton Local Fauna as well as two species of '*Pseudocheirus*' which may (Archer 1984) represent the otherwise modern genus *Petauroides*. Another species of *Pseudochirops*, from the early Pliocene Bluff Downs Local Fauna of northeastern Queensland, is under study (B. Mackness and M. Archer). Pledge (1992) describes a giant species of *Corracheirus* from the late Miocene to Pliocene Curramulka Local Fauna of southern South Australia as well as a single tooth of another large pseudocheirid from the Plio-Pleistocene Cement Mills Local Fauna of southeastern Queensland. Until now, however, no giant pseudocheirids have been reported from undoubted Pleistocene sediments. The tooth described here as *Pseudokoala cathysantamaria*, from early Pleistocene

deposits at Portland, Victoria, is the only ringtail possum confined to the Pleistocene and the only giant ringtail known from the Quaternary.

Fossil koalas (Phascolarctidae) are similarly known from late Oligocene and younger sediments. Stirton (1957), Stirton, Tedford and Woodburne (1967), Woodburne et al. (1987b) and Springer (1987) describe six species in the Oligo-Miocene genera *Perikoala*, *Litokoala* and *Madakoala*. Black and Archer (in press) name another Miocene genus from Riversleigh and Black (in prep.) reports additional Miocene taxa from Riversleigh. Pledge (1992) describes a Miocene to Pliocene species of the giant *Cundokoala*. Bartholomai (1968) describes a large Plio-Pleistocene Queensland species of the modern genus *Phascolarctos*. Pledge (1987a) describes another large *Phascolarctos* from the early Pliocene of South Australia. We describe here isolated teeth, from Pleistocene deposits of Wellington Caves, New South Wales, that appear to represent the same Miocene/Pliocene South Australian species described by Pledge (1992) as *Cundokoala yorkensis*. The Wellington material includes the first known upper molars for this taxon.

Material described is registered in the palaeontological collections of three institutions as follows: AM F numbers represent the Australian Museum fossil collection; P numbers represent the palaeontological collections of the Museum of Victoria; SAM P numbers represent the palaeontological collections of the South Australian Museum. Dental terminology used here follows Luckett (1993) for molar homology, Flower (1867) for premolar homology and Archer (1984) and Woodburne et al. (1987a,b) for molar morphology.

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Superorder Marsupialia Illiger, 1811

Order Diprotodontia Owen, 1866

Superfamily Phalangerioidea Weber, 1928

Family Pseudocheiridae Winge, 1893

Pseudokoala Turnbull and Lundelius, 1970

Type species:

Pseudokoala erlita Turnbull and Lundelius, 1970

Additional species:

Pseudokoala curramulkensis (Pledge, 1992) and *Pseudokoala cathysantamaria* n. sp.

Revised generic distribution:

Corra Lynn Cave, Yorke Peninsula, South Australia; Hamilton Local Fauna, southwestern Victoria; Portland Local Fauna, Nelson Bay Formation, Portland, Victoria.

Revised age range for the genus:

The Hamilton Local Fauna is interpreted (Rich et al. 1991) to be early Pliocene in age. The Curramulka Local Fauna is interpreted (Pledge 1992) to be late Miocene to Pliocene in age; the Nelson Bay Formation is interpreted (Flannery and Hann 1984) to be early Pleistocene in age.

Revised generic diagnosis:

Species of *Pseudokoala* are distinguished from *Marlu praecursor* by their continuous postmetacristid and preentocristid, and posthypocristid which does not extend to the

lingual side of the crown. They are distinguished from *M. kutjamarpens* by their continuous postmetacristid and preentocristid, connection of the cristid obliqua to the metacristid and their truncated posthypocristid. They are distinguished from species of *Pildra* and *Paljara* in their lack of an entostylid, presence of a buccal buttress on the protoconid, *en echelon* overlap of the postmetacristid and preentocristid, large size, and truncated posthypocristid. They are distinguished from species of *Pseudocheirus*, *Petauroides* and *Hemibelideus* in having a truncated posthypocristid, being much larger in size, having a second buccal buttress on the protoconid, not having steep entoconid blades and in lacking a protostylid. They are distinguished from species of *Pseudochirops* in having a truncated posthypocristid, being larger in size, having a second buccal buttress on the protoconid, not having steep entoconid blades, having the cristid obliqua connected to the metacristid, and in lacking a protostylid.

Pseudokoala curramulkensis (Pledge, 1992)

Emendation of dental homology for the paratype and referred specimen:

Pledge (1992) notes three specimens including the Holotype. The homology of the teeth (using the M1-4 molar homology system of Luckett 1993) given in table 5 needs emendation as follows. SAM P29901 (referred specimen) is a right dentary fragment with M₂ (not M₁) and alveoli for M₁ and M₃₋₄. SAM P31792 (Paratype) is a left dentary fragment with M₂₋₃ (not M₁₋₂) and alveoli for M₁ and M₄.

Pseudokoala cathysantamaria n. sp.

Holotype:

P173650, an isolated LM₁ (Fig. 1).

Type Locality:

Interpreted to be Nelson Bay, Portland, Victoria, although no specific locality details are recorded in the Museum of Victoria Palaeontology register (B. Thompson, pers. comm. to M. Archer), nor are there any details on the specimen label. However, it is registered within a series of fossils, including P173649 (a dentary of *Pseudocheirus* sp. cf. *P. peregrinus*; see below), for all of which the locality data is Nelson Bay, Portland, Victoria.

Age:

Marine invertebrates from the Lower Nelson Bay Formation, the probable source of the Holotype, are early Pleistocene in age (Flannery and Hann 1984).

Etymology:

In honour of Cathy Santamaria for her constant interest and much appreciated encouragement for palaeontological research in Australia.

TABLE 1

Measurements of *Pseudokoala* material. All measurements in millimetres.

Specimen	P3		M1			M2			M3			M4		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
MV P173650			10.7	5.20	5.60									
SAM P26542			10.9	4.51	5.20									

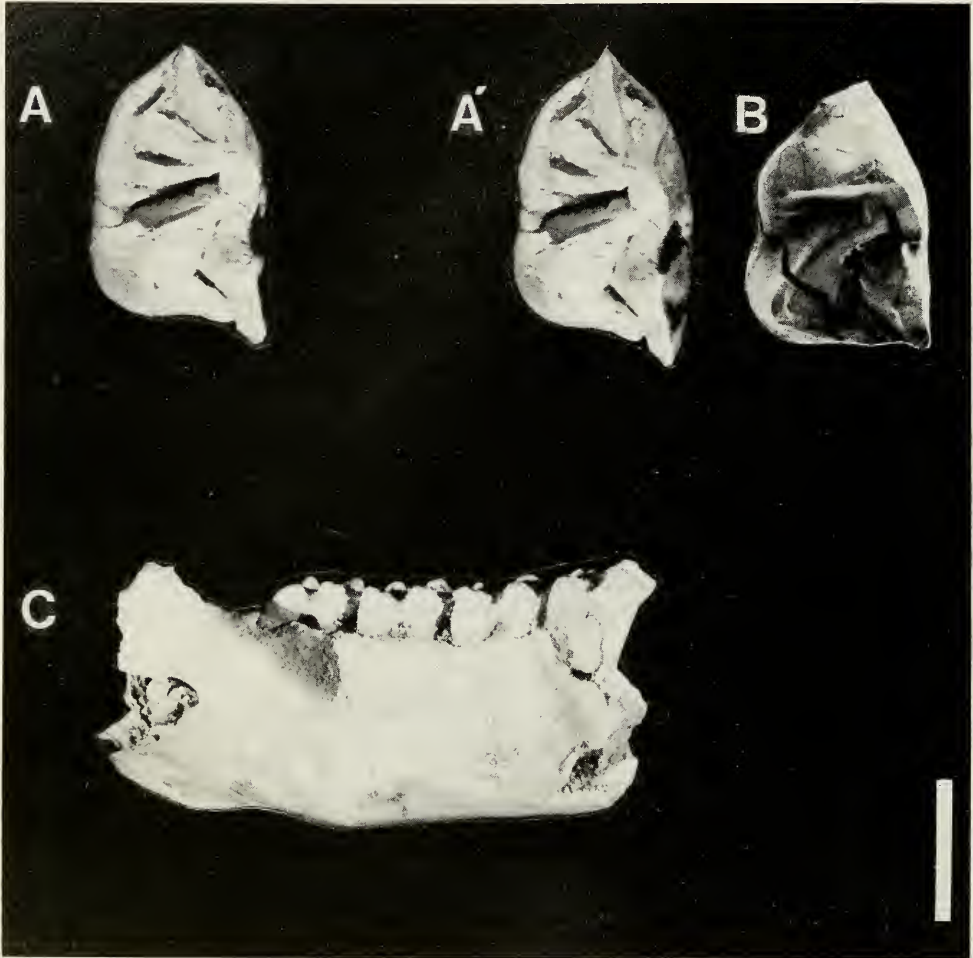


Figure 1. A-A', Holotype of *Pseudokoala cathysantamaria* n.sp, Museum of Victoria P173650, occlusal stereopair of left M_1 , from the early Pleistocene of Portland, Victoria; B, *Pseudokoala erlita*, NMV P54159, left M_1 , occlusal stereopair; C, *Pseudocheirus* sp. cf. *peregrinus*, Museum of Victoria P173649, a right dentary fragment with M_{1-4} , from the early Pleistocene of Portland, Victoria. Bar indicates 5mm.

Species diagnosis:

Pseudokoala cathysantamaria is a giant ringtail possum with molar teeth at least 20% larger than those of *P. erlita* (Turnbull et al. 1987) but comparable in size (Table 1) to *P. curramulkensis* (Pledge 1992; see below). It is also distinguished from *P. erlita* by having an extra anterior vertical buttress (as well as a posterior one) on the buccal flank of the protoconid, an anterobuccal vertical trigonid cleft anterior to the extra vertical buttress, an anterolingual basal cingulum and cingular pocket, a lingually convex metacristid, posterior elongation of the postentocristid, and mesostylids between the bases of the hypoconid and protoconid. Although the missing anterior half of M_1 for *P. curramulkensis* prohibits comparisons in this area, the tooth of *P. curramulkensis* is smaller, appears to lack at least the posterior mesostylid, may lack the anterior flexure on the cristid obliqua, and has a much shorter postentocristid. In this feature, the three species appear to form a gradient with the postentocristid of *P. erlita* the least extended and that of *P. cathysantamaria* the most.

Description:

The Holotype (Fig. 1) is the least worn of any *Pseudokoala* specimen known enabling details of dental morphology in the genus to be clarified. M_1 has a large, medially situated protoconid (as in *P. erlita*) which is connected by a steep anterior paracristid to a tiny possible paraconid (not evident in *P. erlita* and unknown for *P. curramulkensis*), and by a gently inclined posterior metacristid to a poorly distinguished metaconid (as in at least *P. erlita*). Two prominent, vertical buccal buttresses subtend the protoconid. There is a tiny, anterolingual basin defined by a small, basal anterolingual cingulum, an anterobuccal cingula and a marked, vertical, anterobuccal trigonid cleft. Between the cristid obliqua and posterior buccal buttress are two basal mesostylids.

The following features of *P. cathysantamaria* are also evident (where they can be checked) in the holotype of *P. curramulkensis* and *P. erlita*. There is no protostylid. At the posterior end of the metacristid is a topographically defined metastylid immediately buccal to the anterior end of the preentocristid. The cristid obliqua does not run directly to the metacristid but instead veers anterobuccally to tangentially contact the metacristid. There are pronounced crenulations on the lingual side of the cristid obliqua. There is *en echelon* overlap of the postmetacristid over the preentocristid. The paracristid, metacristid and postentocristid are elongate and together define a composite blade that extends the length of the whole tooth. The entoconid blades are not steeply inclined. There is no entostylid. The posthypocristid is truncated at the lingual end before it reaches the postentocristid. It stops far short of the posterolingual corner of the tooth, leaving the posterior end of the postentocristid (which extends posteriorly further than the same crest in the other species of *Pseudokoala*) to define the edge of the crown. In terms of relative height on the crown, the protoconid is just higher than the metaconid which is higher than the entoconid which is higher than the metastylid which is higher than the hypoconid which is higher than the paraconid.

Discussion:

Estimates of body size for *Pseudokoala cathysantamaria*, based on tooth and body size in *Phascolarctos cinereus*, suggest that this ringtail may have weighed 9–10 kg, far larger than any living ringtail possum. However, it is only slightly larger than the Curramulka giant ringtail described by Pledge (1992) as *Corracheirus curramulkensis*. Pledge (1992) suggests that species of *Corracheirus* (viz. *C. curramulkensis*) are differentiated from those of *Pseudokoala* (viz. *P. erlita*) by three features: 1, larger size; 2, having the postprotocristid continuous with the cristid obliqua rather than extending to the metastylid; and 3, having a continuous entocristid with a simple metastylid flexure.

Large size is not normally regarded to be a basis for establishment of a monotypic genus (in this case for *curramulkensis* Pledge). Considering the second feature, there are three specimens of *P. curramulkensis* noted in the type description: the Holotype with part of M_1 and M_{2-4} , and SAM P29901 with M_2 which support the distinction with the postprotocristid appearing to make no contact with the metastylid; and SAM P31792 with M_{2-3} where the postprotocristid bypasses (but is touched by) the cristid obliqua to make contact with the metastylid flexure. Consequently, this feature appears to be variable and does not distinguish species of *Corracheirus* from those of *Pseudokoala*. Considering the third distinguishing feature, the Holotype and SAM P29901 do support the suggestion that the preentocristid is continuous with metacristid via a simple metastylid flexure. However, the condition in SAM P31792 is much closer to the *P. erlita* condition in that there is only a very tenuous direct connection linking the preentocristid and the metacristid via a fine and low bridge of enamel buccal to the metastylid. In this specimen, the preentocristid and metacristid really overlap *en echelon*, with the preentocristid passing anterobuccal to the posterior end of the metacristid to make contact with the postprotocristid, a condition closer to that seen in *P. erlita*.

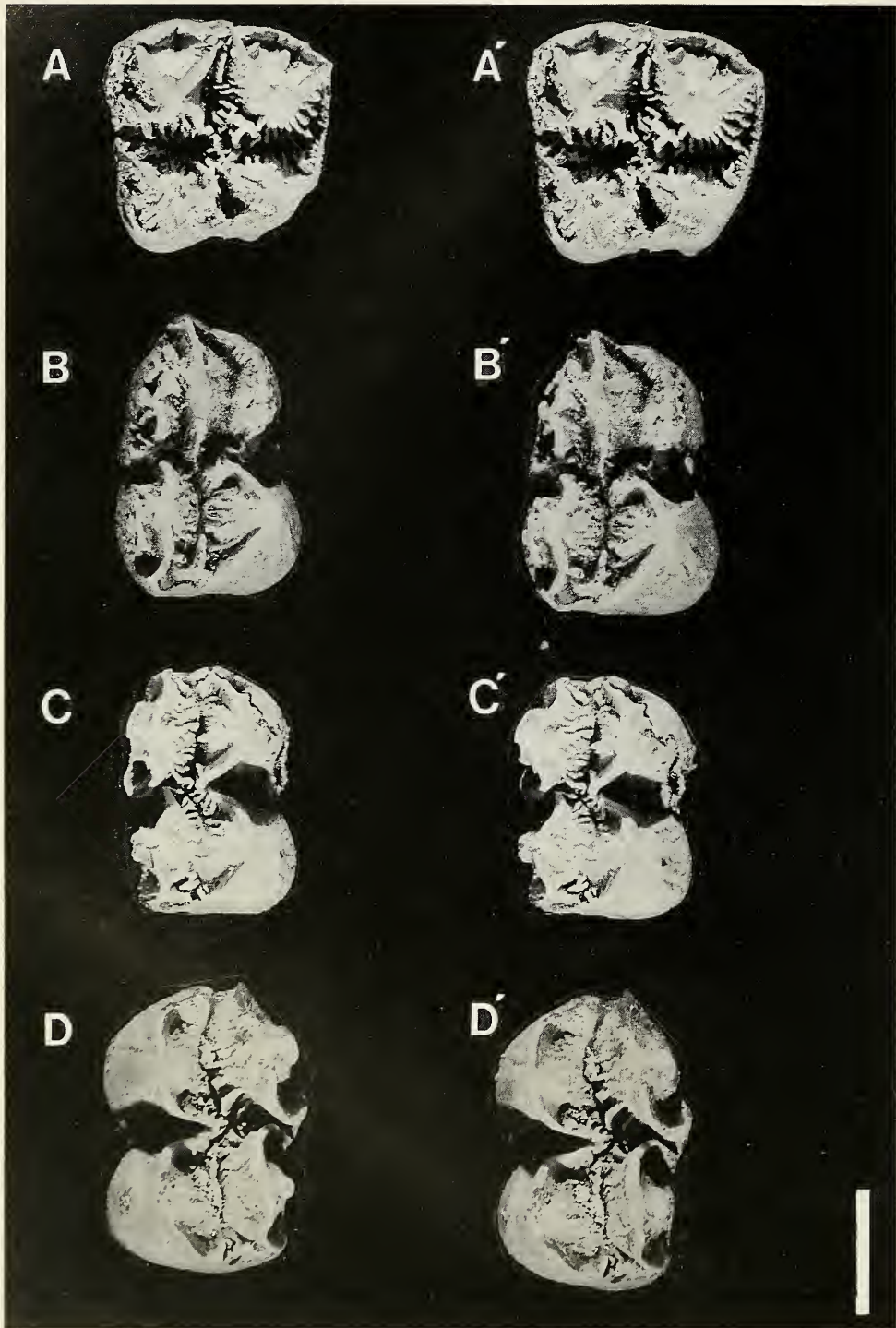


Figure 2. *Cundokoala yorkensis*, referred material from Wellington Caves, New South Wales. A-A', AMF98885, a left M_1^1 . B-B', AMF98886, a right M_1 . C-C', AMF98889, a right M_2 . D-D', AMF98890, a left M_3 . Bar indicates 5mm.

Conversely, comparison of SAM P31792 with the M_3 or 4 of *P. erlita* illustrated in Turnbull, Rich and Lundelius (1987, Fig. 2C) suggests basic overall similarity in all key features (except, possibly, the degree to which the metacristid is lingually concave and the degree of posterior development of the postentocristid; see below). *Corracheirus curramulkensis*, *P. erlita* and *P. cathysantamaria* also exhibit a striking synapomorphy of M_1 : truncation of the posthypocristid such that it stops well short of the lingual side of the crown and does not contact any other structure. This condition differs from all other pseudocheirids where the posthypocristid closely approximates the postentocristid (or the entostylid) at or near the lingual margin of the tooth. All three taxa also exhibit a tendency to posteriorly extend the postentocristid, a feature best-developed in M_1 . Finally, all three taxa appear to be united in their tendency towards gigantism. For these reasons, we suggest that *Corracheirus* Pledge, 1992 is better regarded as junior synonym of *Pseudokoala* Turnbull and Lundelius, 1970 which then contains three species: *erlita* Turnbull and Lundelius, 1970; *curramulkensis* Pledge, 1992; and *cathysantamaria* Archer, Black and Nettle (this paper), *erlita* being the type species of the genus.

Within *Pseudokoala*, *P. cathysantamaria* appears to be the sister-group of *P. curramulkensis*, these two sharing as synapomorphies extreme gigantism and greater posterior development of the postentocristid. Although the trigonid is unknown for *P. curramulkensis*, that of *P. cathysantamaria* shows two prominent buccal buttresses in contrast to one in *P. erlita*, the second buttress being an autapomorphic condition (or perhaps a synapomorphic condition shared with *P. curramulkensis*). The single buttress of *P. erlita* may be the homologue of the vertical protostylid ridge in the same position in species of *Marlu* (or the homologue of the protostylid in, e.g., species of *Pseudocheirus*, *Pseudocheirulus*).

Species of *Pseudokoala* share distinctive features of M_1 with species of *Marlu* Woodburne, Tedford and Archer, 1987 including: failure of the cristid obliqua to directly contact the postmetacristid (a deep crevice intervening); a crenulated cristid obliqua; *en echelon* overlapping of the postmetacristid and the preentocristid (in *M. kutjampensis* but not *M. praecursor*); a vertical buttress but no protostylid on the buccal flank of the protoconid; no entostylid; and gently inclined (rather than steeply inclined) entoconid blades. This intergeneric relationship was originally suggested by Woodburne, Tedford and Archer (1987; Fig. 23) on the basis of synapomorphies exhibited primarily by the upper molars. The new species *P. cathysantamaria* exhibits the same combination of synapomorphies, lending support to the hypothesis of a *Pseudokoala*/*Marlu* clade.

Marked differences between species of *Marlu* and *Pseudokoala* include the truncated posthypocristid of species of *Pseudokoala* and their better-developed entoconid blades. Differences in the nature of the connection between the preentocristid and metacristid vary within at least *P. curramulkensis* (see above) making intergeneric contrasts here of questionable value.

In terms of patristic relationships, the early Miocene *Marlu kutjampensis* exhibits no features that would preclude it being ancestral to the Pliocene/Pleistocene species of *Pseudokoala*.

Pseudocheirus Ogilby, 1837

Pseudocheirus sp. cf. *P. peregrinus* (Boddaert, 1785)

Specimen:

P173649, a right dentary with M_{1-4} (Fig. 1).

Locality:

Nelson Bay, Portland, Victoria. Label data also records: 'Monash Univ. field trip (1973?)' and '# 280 004'.

Age:

The marine invertebrate assemblage of the Lower Nelson Bay Formation, source of P173649, is early Pleistocene in age (e.g., Flannery and Hann 1984).

Description:

P173649 is a *Pseudocheirus peregrinus*-sized ringtail possum (Table 2) with overall similarity to *P. peregrinus* and *P. occidentalis*. It is, however, distinguished from these modern species (most individuals but not all, these features being somewhat variable in at least *P. occidentalis*) in that: the preentocristid is connected to the metastylid on M_{2-4} ; and the metaconid on M_1 is less distinct. It is distinguished from *Pseudocheirus herbertensis* in that: the preentocristid is connected to the metastylid; the M_1 lingual parastylid is not developed; and there is no notch between the postmetacristid and metastylid. It is distinguished from *P. caroli* and *P. forbesi* in that: the preentocristid is connected to the metastylid; the M_1 lingual parastylid is not developed; the preentocristid is strongly bladed; and there is no notch between postmetacristid and metastylid. It is distinguished from *P. canescens* and *P. mayeri* in that: the preentocristid is connected to the metastylid; the preentocristid is strongly bladed; and there is no notch between postmetacristid and metastylid. It is distinguished from *Hemibelideus lemuroides* in that: the buccal shelf is not prominent; and the M_1 metaconid is less distinct. It is distinguished from *Petauroides volans* in that: the preentocristid is connected to the metastylid; there is no entostylid ridge; and the M_1 metaconid is less distinct. It is distinguished from *Pseudochirops albertisii* in: not having a protostylid basin on M_1 ; lacking a prominent buccal shelf; lacking an entostylid ridge; lacking a posterobuccal trigonid basin; and in having a less distinct M_1 metaconid. It is distinguished from *P. corinnae* in that: the preentocristid is connected to the metastylid; it lacks a protostylid basin on M_1 ; it lacks a prominent buccal shelf; it lacks an entostylid ridge; it has no posterobuccal trigonid basin; and the M_1 metaconid is less distinct. It is distinguished from *P. cupreus* in: not having a protostylid basin on M_1 ; lacking a prominent labial shelf, the M_4 cristid obliqua is not angulate, no entostylid ridge, no posterobuccal trigonid basin; and in having a less distinct metaconid on M_1 . It is distinguished from *P. archeri* in: not having a protostylid basin on M_1 ; having an M_4 cristid obliqua that is not angulate; lacking an entostylid ridge; lacking a posterobuccal trigonid basin; and in having a less distinct metaconid on M_1 . It is distinguished from *Petropseudes dahli* in: not having a protostylid basin on M_1 ; lacking a prominent buccal shelf; lacking a posterobuccal trigonid basin; and in having a less distinct metaconid on M_1 . It is distinguished from the species of all extinct ringtail genera in having: a well-developed M_1 protostylid; a preentocristid connected to the metastylid; a strongly bladed preentocristid; an entoconid that is positioned anterior to the hypoconid; a protoconid positioned lingual to the midline of M_1 ; and a less distinct metaconid on M_1 .

TABLE 2

Measurements of *Pseudocheirus* material. All measurements in millimetres.

Specimen	P3		M1			M2			M3			M4		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
MV P173649			4.16	1.96	2.22	4.06	2.15	2.30	4.05	2.15	2.27	4.36	1.88	2.15
AM M4046	3.51	1.58	3.98	1.74	2.29	3.84	2.12	2.54	4.03	2.37	2.60	4.74	2.43	2.30

The early Pleistocene habitat of Portland:

The presence of an ektopodontid and *Pseudokoala cathysantamaria* in the Portland assemblage suggests a rainforest component in the palaeoenvironment. All ektopodon-

tids occur in assemblages that have been interpreted (e.g. Archer, Hand and Godthelp 1995) to represent rainforest communities or communities that include rainforest: the late Oligocene Ditjimanka and Ngama Local Faunas, South Australia; the early and middle Miocene assemblages of Riversleigh, Queensland; the ?early or middle Miocene Kutjamarpu LF, South Australia; and the early Pliocene Hamilton LF, Victoria. The late Miocene to Pliocene Curramulka LF of South Australia, which contains *Pseudokoala curramulkensis*, is also regarded (Pledge 1992) to represent wet sclerophyll forest and/or rainforest, as is the Hamilton assemblage (Turnbull and Lundelius 1970, Turnbull, Rich and Lundelius 1987) which contains *P. erliia*. The occurrence in the Portland assemblage of *Pseudocheirus* sp., cf. *P. peregrinus* does not conflict with this interpretation because, although primarily an inhabitant of dense understorey vegetation, some modern populations of *P. peregrinus* extend well into rainforest.

Order Diprotodontia Owen, 1866

Suborder Vombatiformes Woodburne, 1984

Infraorder Phascolarctomorpha Aplin and Archer, 1987

Family Phascolarctidae Owen, 1839

Cundokoala yorkensis Pledge, 1992

Holotype:

SAM P24904, left dentary with M₁₋₄ and alveolus for P₃.

Referred material

(Fig. 2) and (Table 3): SAM P24905, partial left M₄ in its alveolus.

AM F98885, L M₁; AM F98886, R M₁; AM F98887, L M₂; AM F98888, L M₂; AM F98889, R M₂; and AM F98890, L M₃.

TABLE 3

Measurements of all known specimens of *Cundokoala yorkensis*. All measurements in millimetres.

Abbreviations: L, length; AW, anterior width; PW, posterior width.

Specimen	P ³			M ¹			M ²			M ³			M ⁴		
	L	W		L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
AM F98885				12.1	12.3	11.0									
	P ₃			M ₁			M ₂			M ₃			M ₄		
	L	W		L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
P24904				11.8	7.0	8.1	12.9	8.1	8.1	12.9	8.0	8.2	12.7	7.4	7.3
AM F98886				11.5	6.5	8.0									
AM F98887							11.5	6.9	6.8						
AM F98888							11.2	7.2	7.0						
AM F98889							11.3	7.1	6.9						
AM F98890										11.4	7.3	6.7			

Revised distribution:

Cundokoala yorkensis is known from Corra Lynn Cave, the Curramulka Local Fauna, Yorke Peninsula, South Australia and now Wellington Caves, New South Wales.

Revised age range:

The Curramulka Cave site of the typical material is interpreted by Pledge (1992) to be Miocene to Pliocene in age. The exact locality and age for all but one (AM F98886) of the Wellington Caves specimens is unknown. They were collected from the surface of spoils piles dumped outside the newly restored entrance to the Phosphate Mine. The material on these piles had been obtained during excavation of tourist paths in the Wellington Caves complex in late 1995. The source of the material for each pile was not certainly known but thought by excavation workers at the site to be various localities within the Phosphate Mine and Bone Cave. Although most of the taxa recovered to date from the Wellington Caves complex of sediments have been interpreted to be Pleistocene in age, Hand, Dawson and Augee (1988), L. Dawson et al. (in prep.) and Osborne (1983) have demonstrated that some deposits in the Wellington Caves complex (e.g., in the entrance doline of Big Sink and others in the Phosphate Mine) are Pliocene in age. Therefore the age of the *Cundokoala yorkensis* material obtained from the spoils piles could be Pliocene, Pleistocene or both.

AM F98886, however, was obtained by one of us (MA) in company with H. Godthelp, A. Gillespie, A. Musser et al. from a newly-excavated pathway in the Phosphate Mine. Material excavated at the same time included an isolated lower molar of *Diprotodon* sp. cf. *D. optatum* (only known from the Pleistocene), a dentary of *Protemnodon* sp. cf. *P. roechus* (only known from the Pleistocene), abundant dentary and maxilla fragments of *Aepyprymnus rufescens* (Pleistocene and living species) and a dentary of *Onychogalea unguifera* (living species). Although other taxa obtained at the same time have yet to be identified, nothing contradicts a Pleistocene age for this assemblage. We would conclude, pending a thorough analysis of the rest of the fauna from this deposit, that Wellington Caves *C. yorkensis* is Pleistocene in age, giving the species a Pliocene-Pleistocene age range.

Revised diagnosis

Cundokoala yorkensis differs from all other phascolarctids: in being larger; having higher-crowned teeth; and in having a relatively short, massive dentary. It differs from all other phascolarctids except species of *Phascolarctos* in having: a larger paraconule and neometaconule on M^1 ; a more lingually positioned protoconid and a larger protostylid on M_1 ; well-developed lingual columnar stylids on the metaconid and entoconid of M_{1-4} ; and a well-developed buccal cingulum and metastylid fold on M_{1-4} . It differs from species of *Litokoala* in: lacking the posterobuccal crest which extends from the apex of the metaconid in M_{2-4} ; lacking an anteriorly displaced entoconid (relative to the hypoconid) on M_4 ; lacking an anteriorly displaced metaconid (relative to the protoconid) on the M_4 ; and in having the postprotocristid and cristid obliqua of M_4 meeting in the transverse median valley on M_4 (in contrast to the parallel arrangement seen in *Litokoala kanunkaensis*). It differs from species of *Madakoala* and *Perikoala*: in having: a larger parastyle on M^1 ; a more crenulate, less linearly-oriented paraconule and neometaconule on M^1 ; a paraconule that connects anterobuccally to the anterior cingulum on M^1 ; an entostylid ridge on M_{1-4} ; a more lingual junction of the postprotocristid and cristid obliqua; and in lacking protoconid-metaconid and hypoconid-entoconid crests.

Description

The new Wellington Caves materials (AM F98885 to AM F98890) augment understanding about the morphology of this species. AM F98885 is an unworn, relatively square selenodont M^1 that tapers posteriorly. It is morphologically very similar to the M^1 of species of *Phascolarctos* and differs mainly in being relatively wider anteriorly. The paracone and metacone are similar in height and are the tallest cusps on the tooth followed by the metaconule and protocone. The apex of the protocone lies lingually opposite that of the paracone. The apex of the metaconule lies lingually opposite and slightly anterior to that of the metacone. The lingual bases of the paracone and metacone and the anterolingual base

of the protocone are highly crenulate. The protocone and metacone and their associated crests are slightly obliquely (anterolingually) oriented. The tooth is bisected bucco-lingually by a deep transverse median valley and antero-posteriorly by a relatively deep longitudinal valley. The buccal tooth margin is mildly convex sloping anterolingually at the anterolingual tooth margin and curving posterolingually around the buccal margin of the metacone. The lingual bases of the protocone and metacone slope gently towards the base of the crown. The lingual bases of the paracone and metacone slope more steeply into the longitudinal tooth valley. The triangular buccal surface of the paracone is reduced relative to the metacone as is the paracone buccal margin. The buccal basin of the paracone is closed and deep. The buccal basin of the metacone is comparatively shallower but remains closed. A ridge-like styler shelf extends along the length of the buccal tooth margin. The relative heights of styler cusps in descending order are as follows: styler cusp C, B, A, D and E. The preparamacrista, postparamacrista, premetacrista and postmetacrista which make up the buccal selene of the tooth, are distinct linear crests which extend from the apices of the paracone and metacone respectively. The lingual selene is offset posteriorly and is composed of a relatively linear preprotocrista and premetaconule crista and a crescentic postmetacrista and highly crescentic postprotocrista. The postprotocrista and premetaconule-crista meet in the transverse median valley at a point slightly lingual to the longitudinal valley. The parastyle is poorly developed. It exists as a slight swelling of the anterior cingulum at the anterobuccal corner of the tooth. A shallow pocket is created between the anterior cingulum and the anterior base of the paracone. Lingually, the pocket is defined by a small, crenulate, but distinct paraconule which lies at the anterolingual base of the paracone. A short, non-cusate, spur-like protostyle which originates from the preprotocrista at a point slightly lingual to the longitudinal valley, extends posteriorly along the buccal base of the protocone, terminating opposite the protocone apex. A well developed anterolingual paramacrista connects the paraconule posteriorly to the apex of the paracone. A similarly well-developed posterolingual paramacrista extends from the apex of the paracone into the junction of the transverse median and longitudinal valleys wherein it divides into two spurs which become part of the crenulation pattern of the tooth.

A small, crenulate, non-cusate neometaconule lies in the longitudinal tooth valley at the anterolingual base of the metacone. It is connected to the metacone base by a weak anterolingual metacrista, which originates approximately half way down the base of the metacone. A posterolingual metacrista is absent. A crenulate, cingulum-like shelf runs along the anterior and anterolingual base of the protocone forming a shallow pocket between the cingulum and the protocone base. A weak anterolingually directed crest extends from the apex of the protocone to meet the anterolingual cingulum. A similar, but deeper pocket occupies the anterolingual base of the metaconule and is bounded by the posterior base of the protocone anteriorly, the anterior base of the metaconule posteriorly, the junction of the premetaconule crista and postprotocrista buccally, and a short, crescentic lingual cingulum lingually. The lingual cingulum effectively closes off the lingual exit of the transverse median valley and is continuous with a weak crest that extends anterolingually from the apex of the metaconule. Weak buccally directed spurs extend from the apices of the protocone and metaconule, fading down their respective bases towards the longitudinal valley. A well developed posterior cingulum is continuous with the postmetaconulecrista lingually and buccally and meets styler cusp E at the posterobuccal tooth corner.

The M_1 of the holotype is poorly worn and the anterolingual tooth corner is missing. Consequently, much of the crown morphology of the trigonid has been lost. In AMF98886 the preprotocristid is a well defined, linear crest which terminates anteriorly in a small paraconid. The preprotostylidcristid extends anterolingually to terminate at the base of the paraconid. Pledge (1992), in his description of the holotype M_1 , suggests that *C. yorkensis* differs from all other phascolarctids in having a fine anterobuccal spur of the preprotocristid meet the preprotostylidcristid at the anterior tooth margin. Its absence in AM F98886 suggests this is a variable feature within the species, and the prepro-

tocristid spur is most probably part of the crenulation pattern of the tooth. A well-developed posterobuccal ridge extends from the protostylid apex in AM F98886. This crest is only vaguely discernible in the holotype. The buccal cingulum is better developed in AM F98886. The postprotocristid meets the anterior base of the cristid obliqua at a slightly more lingual position than in the holotype. The lingual columnar stylids of the metaconid and entoconid are large, crenulate and well preserved in AM F98886 whereas they are only represented by slight swellings in the holotype. The entostylid is a well-developed, cusped swelling on the terminus of the postentocristid at the posterolingual tooth corner in AM F98886. AM F98887, AM F98888 and AM F98889 (M_2) are morphologically similar to but smaller than the M_2 of the holotype. Again, the holotype is highly worn, the apices of all major cusps are missing and the lingual tooth margin is damaged such that the columnar stylids are not preserved and the entostylid is missing. In contrast, all of the Wellington Caves M_2 specimens show little or no wear. The columnar stylids are large, particularly that of the metaconid. The postentocristid curves lingually to the posterolingual tooth corner where it terminates in a well developed entocristid. The entoconulid, like in the holotype, is poorly developed. Well developed lingually directed crests extend from the apices of the protoconid and hypoconid and terminate just prior to reaching the longitudinal valley. These crests are not present in the holotype. The M_3 , AM F98890, is largely unworn and is slightly smaller than the M_3 of the holotype. The postmetaconid, preentocristid and postentocristid are more arcuate than in the holotype. The lingual buttresses of the metaconid and entoconid are better developed however the buccal bases of these cusps are more greatly expanded in the holotype. The metastylid is larger and the metastylid fold is more pronounced. The lingual faces of the protoconid and hypoconid are more steeply sloping and the lingually directed crests associated with these cusps are well developed (however they are absent in the holotype). Following an analysis of variation in dentitions of the modern species, it is evident that the above mentioned morphological differences between the referred material and the holotype fall within the boundaries of normal intraspecific variation.

DISCUSSION

Pseudokoala cathysantamaria is an enormous ringtail possum and *Cundokoala yorkensis* an enormous koala. With the addition of these two to the Pleistocene of Australia, all families of Australian herbivorous mammals are now known to have had giants in the Pleistocene megafauna. They also significantly increase the ranks of known arboreal megafaunal species. Apart from one modestly large koala (*Phascolarctos stirtoni* Bartholomai, 1968), the only undoubted megafaunal arboreal species previously known from the Pleistocene was *Bohra paulae* Flannery and Szalay, 1982, a gigantic tree kangaroo from Wellington Caves, New South Wales.

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